

## Density-dependent spatial patterning of woody plants differs between a semi-arid and a mesic savanna in South Africa

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### ABSTRACT

Savannas can be defined by the co-dominance of grasses and trees. Interactions between these two life forms are relatively well studied, whereas tree-tree interactions attracted increased attention only recently. However, the influence of woody plant density on tree-tree interactions is rarely considered. We studied tree-tree interactions in a semi-arid and a mesic savanna to test for differences between open and dense woody vegetation in relation to broad-scale environmental conditions. We applied spatial point pattern analysis to gain a better understanding of processes, such as competition, facilitation and disturbances, affecting the spatial distribution of trees. Competition between trees was most pronounced in dense vegetation, whereas facilitation effects were more common in open vegetation. Further, we found that factors shaping the spatial patterns differ with scale. At short tree-to-tree distances, results indicate limited seed dispersal as the most influential factor explaining the spatial distribution of trees. However, with increasing tree-to-tree distances, environmental heterogeneity in the semi-arid savanna and disturbances in the mesic savanna became more important. We conclude that studying tree-tree interactions in savannas should explicitly consider the actual woody plant density, especially when different savanna types are compared.

### 1. Introduction

Savannas represent the largest biome in South Africa as well as on the whole African continent (Rutherford et al., 2006). They are characterized by a continuous grass layer interspersed with scattered trees or shrubs (Scholes and Archer, 1997). The outstanding characteristic of savannas is the co-dominance of the two contrasting plant life forms trees and grasses (Scholes and Archer, 1997). Different savanna types can be classified with respect to the mean annual precipitation (MAP) they receive (Sankaran et al., 2005). In African semi-arid savannas, the MAP is generally < 650 mm/yr and the tree cover is primarily limited by the available soil moisture (Sankaran et al., 2005). The establishment of tree seedlings commonly depends on a sequence of favourable rainfall events and reduced tree-grass and tree-tree competition (Sankaran et al., 2004). Semi-arid savannas are therefore also referred to as climate-dependent savannas (Bond et al., 2003). In contrast, mesic savannas receive > 650 mm/yr MAP, and frequent disturbances such as fire or grazing and browsing are required to prevent canopy closure (Sankaran et al., 2005). Thus, mesic savannas are also referred to as fire-dependent savannas (Bond et al., 2003; Sankaran et al., 2004).

Savanna dynamics and especially the mechanisms allowing the co-dominance of trees and grasses are not fully understood and are still debated (Moustakas et al., 2010; Sankaran et al., 2004). While tree-grass interactions have been a major topic in savanna research (e.g. Accatino et al., 2010; Ward et al., 2013), tree-tree interactions are less commonly studied (House et al., 2003). Additionally, most case studies analysing tree-tree interactions neglect the actual tree density or cover as a potential factor influencing savanna structure (e.g. Meyer et al., 2008; Mureva and Ward, 2016; Pillay and Ward, 2012). However, in order to improve the understanding of savanna dynamics, an improved understanding of not only tree-grass interactions, but also of tree-tree interactions as one major vegetation layer is necessary. Also, studies are generally highly case specific with a lack of cross-site comparisons (House et al., 2003) and do not differentiate between different life-history stages (Sankaran et al., 2004; Ward et al., 2013). Therefore, one possible comprehensive study approach to better understand savanna dynamics is to include tree-tree interactions, different life-history stages and tree densities as well as different savanna types (House et al., 2003; Sankaran et al., 2004).

Such a study requires investigating the effects of tree-tree

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**Table 1**

Overview of summary statistics and null models used to address the hypotheses about different spatial patterning and tree-tree interactions in semi-arid and mesic savannas. For additional 278 information on the null models see Velázquez et al. (2016) and Wiegand and Moloney (2014).

Hypotheses	Summary statistic and null model	Figure/Table
(i) The shift from a clustered pattern to a regular pattern with increasing tree height is more pronounced in the semi-arid savanna compared to the mesic savanna.	Univariate pair correlation function $g(r)$ with CSR for each height group.	Fig. 3 Fig. 5
(ii) The shift from a clustered pattern to a regular pattern with increasing tree height is more pronounced in denser vegetation compared to open vegetation.	Univariate pair correlation function $g(r)$ with CSR for each height group. Mark-correlation function $k_{mm}(r)$ with random marking. Correlation between distance to and mean size of 4 nearest neighbours.	Fig. 3 Fig. 4 Fig. 5 Fig. 6 Table 3 Table 4
(iii) Associations between small and large trees occur in both savanna systems	Bivariate pair correlation function $g_{12}(r)$ with antecedent conditions.	Fig. 7
(iv) Associations between small and large trees are primarily found in open vegetation compared to denser vegetation.	Bivariate pair correlation function $g_{12}(r)$ with antecedent conditions. Mark-correlation function $k_{mm}(r)$ with random marking. Correlation between distance to and mean size of 4 nearest neighbours.	Fig. 4 Fig. 6 Fig. 7 Table 3 Table 4

CSR: complete spatial randomness

interactions, e.g. competition and facilitation effects or seed dispersal limitation, on the spatial distribution of individual trees (Meyer et al., 2008; Mureva and Ward, 2016; Pillay and Ward, 2012). One proven method to study both the spatial distribution of trees and their density-dependent properties, such as position or size, is spatial point pattern analysis. The position (rooting point) of each tree is considered as a point in space and the properties of the overall point pattern such as local density, clustering or the distribution of tree characteristics in a local neighbourhood are analysed on a continuum of different spatial scales (Velázquez et al., 2016; Wiegand and Moloney, 2014). Analysing the point pattern allows deducing the underlying ecological processes forming the spatial pattern of trees (Law et al., 2009; Wiegand and Moloney, 2014). In the present study, the term 'tree' refers to trees and shrubs, whereas their individual rooting points define the spatial point pattern of the woody savanna component. There are three fundamental configurations of spatial point patterns: i) random, ii) clustered/associated or iii) regular/segregated, each of which has an ecological interpretation.

A random pattern of trees is commonly attributed to purely stochastic events without dominant processes shaping the pattern (Wiegand and Moloney, 2014). However, a random pattern may also result from non-random processes such as a superposition of different processes (e.g. limited seed dispersal and simultaneous competition) or represent an intermediate transitional state between clustering and regularity.

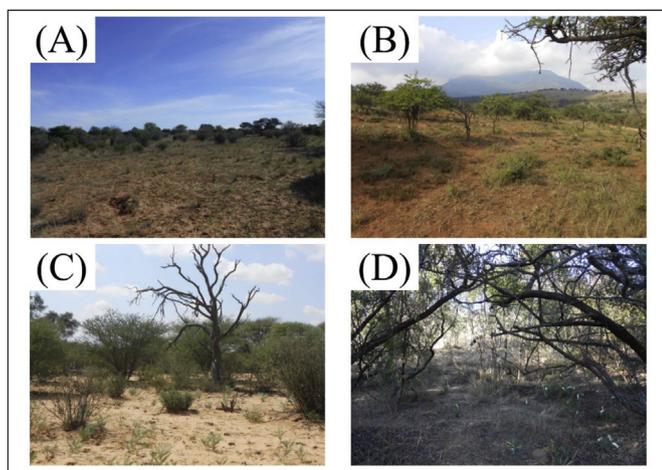
A clustered pattern of trees is commonly attributed to limited seed dispersal (Caylor et al., 2003; Meyer et al., 2008), vegetative propagation (Meyer et al., 2008) or a heterogeneous environment of favourable regeneration sites (Caylor et al., 2003; Meyer et al., 2008). Clustered patterns due to limited seed dispersal are mainly found for young, small trees (Meyer et al., 2008). Facilitation effects may be another reason for a clustered pattern. These facilitation effects include buffering against extreme temperatures, higher soil moisture and nutrient availability, an improved soil structure or protection from herbivory. Facilitation can also lead to an association between small and large trees, because smaller trees may benefit from the special micro-environment in the subcanopy of larger trees. Such effects are more common in arid and semi-arid ecosystems than in more moist environments (Flores and Jurado, 2003). In mesic savannas, clustering of trees may result from frequent fires or grazing and browsing impacts. Tree clusters suppress the grass growth and hence the fire probability and intensity, thereby limiting the ignition and spread of fires (Accatino et al., 2016; Skarpe, 1991). Consequently, small trees, which are most susceptible to fire (Scholes and Archer, 1997), are less likely to be killed

by fire in the neighbourhood of larger trees as large trees reduce the fire intensity.

A regular pattern is commonly attributed to competition effects (Meyer et al., 2008). Competition is the negative influence on a tree exerted by one or several neighbouring trees (Fowler, 1986). At this, the weaker competitor is usually smaller in size or not able to establish or survive (Pielou, 1962; Shackleton, 2002). The latter can be the result of 'density-dependent mortality'. Density-dependent mortality is often assumed to be more common in dense woody vegetation due to increased competition (e.g. dense forests), but can also be present in encroached or thickened savannas (Sea and Hanan, 2012; Wiegand et al., 2008). A regular pattern is expected for older, larger trees because of their increased competitive strength and space demand leading to a maximization of tree-to-tree distances between mature trees (Wiegand et al., 2006). If density-dependent mortality is present, the spatial pattern of small trees should be more clustered, whereas for large trees the spatial pattern should be more regular (in the following we refer to this change in patterning as 'shift' from clustered to regular with increasing tree size). However, density-dependent mortality may be more common in savanna systems without reoccurring disturbances because disturbances, such as fire and grazing or browsing, reduce tree-tree competition (Sea and Hanan, 2012) and promote clustering (Accatino et al., 2016; Skarpe, 1991).

To analyse tree-tree interactions comprehensively, we test four hypotheses about the spatial patterning of trees in different savanna types (semi-arid vs. mesic savanna) and with different tree densities each (open vs. dense vegetation) (Table 1). This approach allows us to learn about possible tree-tree interactions without relying on long-term field observations or experiments. The comparison of climatically different savanna types enables us to deduce the potential influence of broad-scale environmental conditions and to infer the importance of the disturbances and mechanisms being generally characteristic within these climates. The comparison of different tree densities allows us to analyse the degree to which point patterns and tree-tree interactions are density-dependent. We tested the following hypotheses:

- (i) The woody savanna layer generally shows a shift from a clustered pattern of small trees to a regular pattern of larger trees likely, due to limited seed dispersal and competition. These patterns are more pronounced in the semi-arid compared to the mesic savanna as a result of less frequent fires.
- (ii) The shift from a clustered pattern to a regular pattern is less pronounced in open vegetation compared to denser vegetation, due to competition being less important in open vegetation.



**Fig. 1.** Dry season aspect of the (A, B) open study sites and the (C, D) dense study sites in the semi-arid savanna (left) and mesic savanna (right).

- (iii) Associations between small and large trees occur in both semi-arid and mesic savannas, most likely related to facilitation in the semi-arid savanna and to disturbances (especially fire) in the mesic savanna.
- (iv) Associations between small and large trees are density-dependent, and thus primarily found in open vegetation compared to dense vegetation, due to competition being less important in open vegetation.

## 2. Methods

### 2.1. Study areas

We chose two study areas in the savanna region of South Africa, one representing a semi-arid savanna (S 25°47', E 22°53') and one representing a mesic savanna (S 27° 30', E 31°19'). In each study area, we identified two study sites in nature reserves, one representing a fairly open savanna and one a comparatively dense savanna of the same vegetation type (Fig. 1). Note, however, that 'dense' does not mean a bush encroached state approaching canopy closure. The vegetation in the reserves was considered at least semi-natural with a minimum of human disturbances.

The study sites in the semi-arid savanna were located within the Molopo Nature Reserve in the North-West Province. The climate is characterized by a MAP of about 300 mm/yr falling mainly from December to March and a mean annual temperature of about 19 °C (Harmse et al., 2016; Rutherford et al., 2006). The deep sandy soils (> 1.2 m) have poor features with respect to soil organic matter, nutrients and water holding capacity (Jones et al., 2013; Rutherford et al., 2006). Rutherford et al. (2006) describe the vegetation type as 'Molopo Bushveld'. The area was used for cattle ranching, but since the declaration as a nature reserve in 1987, no further agricultural management or similar activities have been carried out (Thiele et al., 2008).

In the mesic savanna, the two study sites were located within the Ithala Game Reserve in the northern part of the KwaZulu-Natal Province. The MAP of 792 mm/yr falls mainly from November to May (Mucina et al., 2006). The mean annual temperature recorded at a nearby weather station is about 22 °C (van Rooyen and van Rooyen, 2010). The soils are coarse-grained shallow soils over hard rock with a poor nutrient supply that is limited to the top soil layer and a low water holding capacity (Jones et al., 2013; van Rooyen and van Rooyen, 2010). Mucina et al. (2006) describe the vegetation type as 'Ithala Quartzite Sourveld', which represents an intermediate type between the grassland and the savanna biomes. The reserve was established in 1973. Before that, the area was used for agricultural purposes, especially the

grasslands (Gordijn and Ward, 2013).

In both nature reserves, wild herbivore communities include common grazer and/or browser species like eland (*Taurotragus oryx*), gemsbok (*Oryx gazella*), and zebra (*Equus quagga burchellii*) among others (Thiele et al., 2008; van Rooyen and van Rooyen, 2010). Megaherbivores such as elephants (*Loxodonta africana*) were exclusively present at the Ithala Game Reserve and are known to have impacts on the vegetation structure by toppling trees (Midgley et al., 2005). However, at the study sites no such impacts on the woody vegetation were observed.

### 2.2. Site selection and mapping of trees

Vegetation sampling at the study sites took place from March to May 2016. The main criteria for the site selection were homogeneity with respect to topography, soil type, vegetation composition and structure. All potential confounding factors like watering points, roads or other infrastructure were avoided. Site selection was non-random with the help of local park staff to sample savanna in pristine condition at the greatest possible extent. At the semi-arid sites, there were hardly any natural fires within the last 20 years at least, according to park management. The open site and dense site, however, were affected by a controlled burning in 2002 and 2012, respectively. The fire frequencies at the mesic savanna sites were much higher. Controlled burns were carried out approximately every two years, at the open site last in 2015 and at the dense site last in 2013.

At each study site, we mapped all trees in a plot of varying size and shape (Fig. 2). The dimensions of the plots depended on the density and distribution of trees. According to the requirements of point pattern analysis, more than 70 individuals of the predominant tree species were mapped in each plot (Wiegand and Moloney, 2014). The minimum height of the trees recorded was 5 cm to ensure establishing seedlings and small saplings in the woody recruitment layer were included in the data. In doing so, all trees were recorded non-randomly and contiguously (without spatial interruption). We mapped the trees using two different methods. Firstly, we used the Interpoint method according to Boose et al. (1998) to determine tree coordinates using the distance to three already measured 'reference trees'. For the first three trees, Global Navigation Satellite System (GNSS) coordinates were used. Secondly, we used polar coordinates (Moeur, 1993) and measured the angle  $\alpha$  and the distance  $d$  to a GNSS coordinate. We measured plant height to the nearest 5 cm using range poles. The height values for the semi-arid and mesic savanna sites were sorted separately in increasing order and divided into three equally sized height groups ('small', 'medium', 'large') using the 33rd and 66th quantiles. We used quantiles for both technical and ecological reasons. Technically, quantiles guarantee that each height group contained enough individuals to analyse the data regardless of the absolute height distribution. Ecologically, this approach describes size hierarchies specific to each savanna type. In the semi-arid savanna, small trees were < 0.80 m and large trees  $\geq$  1.90 m in height. In the mesic savanna, small trees were < 0.25 m and large trees  $\geq$  0.50 m in height. Along with the height, we also used the canopy area to characterise the tree size for nearest neighbour analysis, because competition may differentially affect tree height and canopy area. We approximated the canopy area by measuring the major axis  $d_1$  and the minor axis  $d_2$  of the crown and by calculating the canopy area  $A$  as an ellipsoid  $A = (d_1 \cdot d_2 \cdot \pi) / 4$ .

### 2.3. Statistical analysis

Spatial point pattern analysis was performed to analyse the spatial pattern of trees for each plot. We mainly used functions that summarise and describe the spatial characteristics of patterns as a function of tree-to-tree distances  $r$ , i.e. so-called second-order summary functions (Velázquez et al., 2016). An advantage of these summary functions is that they are able to describe scale-specific details of mixed patterns. An

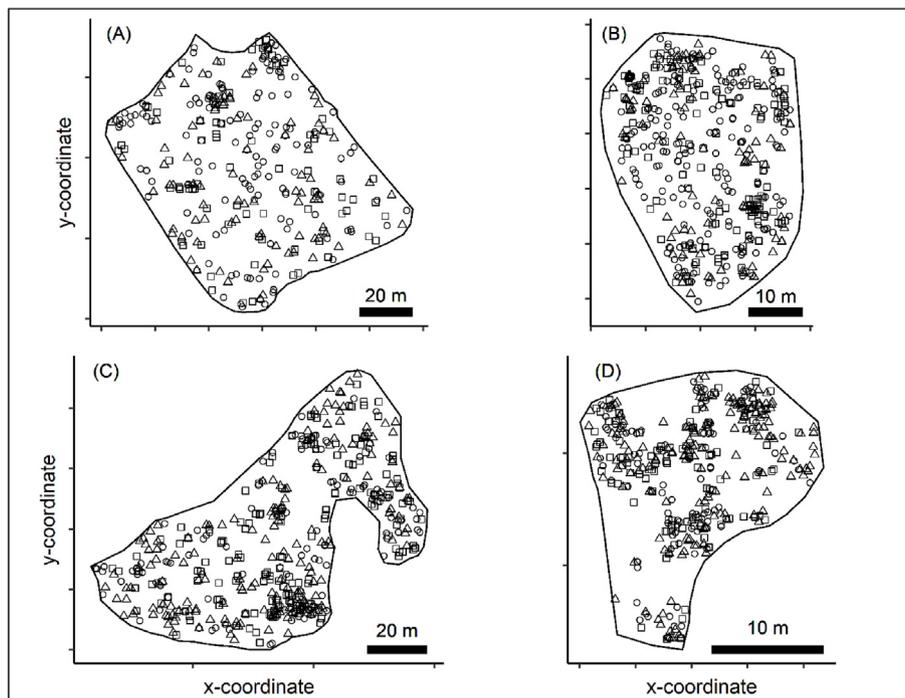


Fig. 2. Spatial distribution of trees in (A, B) the open plots and (C, D) the dense plots in the semi-arid savanna (left) and the mesic savanna (right). Symbols indicate the height groups (circles = small, squares = medium, triangles = large).

example of a mixed pattern is a pattern that is clustered at shorter tree-to-tree distances but regular at larger tree-to-tree distances (Wiegand and Moloney, 2014). This is an advantage because ecological processes are spatially explicit and scale-dependent (Law et al., 2009; Wiegand and Moloney, 2014). We assumed that the environmental conditions and underlying processes are similar within a plot and for all cardinal directions around each tree, i.e. homogeneity and isotropy (Wiegand and Moloney, 2014).

In order to analyse the spatial configuration of the woody vegetation layer, we used the univariate  $g(r)$  and bivariate pair-correlation function  $g_{12}(r)$  (Stoyan and Stoyan, 1994). Univariate implies that each point of the pattern is treated equally, bivariate means that two different types of points (in our case the different height groups) are distinguished (Velázquez et al., 2016). Uni- and bivariate pair-correlation functions are

$$g(r) = \frac{K'(r)}{2\pi r} \quad (1)$$

and

$$g_{12}(r) = \frac{K_{12}'(r)}{2\pi r}, \quad (2)$$

respectively, where  $K'$  is the derivative of Ripley's  $K$ -function (Ripley, 1977). While Ripley's  $K$ -function calculates the expected number of points within distance  $r$  of an arbitrary point of the pattern, the pair-correlation function calculates the expected number of points at distance  $r$  at an arbitrary point. An advantage of the pair correlation function over the  $K$ -function is that it provides a scale-specific description of the pattern; i.e. the value of the pair-correlation function for a specific distance  $r$  is not influenced by properties of the pattern at smaller distances (Wiegand and Moloney, 2014). Hence,  $g(r)$  describes in a straightforward way whether a point pattern is clustered/associated (many points at distance  $r$ ) or regular/segregated (few points at distance  $r$ ) (Wiegand and Moloney, 2014). Note that we used the terms 'clustering' and 'regularity' for univariate patterns and 'association' and 'segregation' for bivariate point patterns (i.e. where two different types of points are distinguished; e.g. small and large trees).

We applied different techniques to detect competition and facilitation by analysing the spatial distribution of tree heights. The mark correlation function compares the mean tree height of two trees separated by distance  $r$  to the overall mean tree height (Stoyan and Stoyan, 1994; Velázquez et al., 2016). Thus, it is able to detect spatial correlations in plant height, e.g. clusters of large trees which may be created by facilitation. The mark-correlation function is calculated as

$$k_{mm}(r) = \frac{E[uv][m(u)*m(v)]}{E(M, M')} \quad (3)$$

where  $E[uv]$  is the expectation that two points are at location  $u$  and  $v$  separated by distance  $r$ , and  $m(u)$  and  $m(v)$  are the corresponding marks of the two points. The denominator  $E(M, M')$  includes random marks from an identical distribution and serves as normalization factor (to result in  $k_{mm}(r) = 1$  for the null hypothesis) (Baddeley et al., 2015).

We also conducted nearest neighbour analysis using the correlation between the distance to the nearest neighbour and the size of the neighbour (Pielou, 1962). To quantify the correlation between these two paired data sets, we used the non-parametric Kendall's rank correlation coefficient  $\tau$ . Values of  $\tau = -1$  and  $\tau = 1$  indicate perfect negative and positive correlation, respectively, and  $\tau = 0$  indicates no correlation. Kendall's  $\tau$  ranks both sets of observations (nearest neighbour distance and size of the nearest neighbour). For concordant pairs both observations are ranked in the same position, for discordant pairs the rankings disagree. The concordant and discordant pairs are used to calculate  $\tau = \frac{c-d}{n(n-1)/2}$ , where  $c$  is the number of concordant pairs,  $d$  is the number of discordant pairs and  $n$  is the number of total observations (Bolboacă and Jäntschi, 2006). However, because in reality the nearest neighbour is not necessarily the only or the most important competitor, we used the sum of the sizes and the sum of the distances to the four nearest neighbours (Shackleton, 2002).

The maximum distance,  $r_{\max}$ , up to which we calculated the second-order summary statistics depended on the plot area, i.e.  $r_{\max}$  equalled one-quarter of the shortest side of the rectangle enclosing the plot (Baddeley et al., 2015). The edge region disobeys points outside the plot that influence the individuals near to the edge and thereby the pattern (Wiegand and Moloney, 2014). Therefore, there is a need for edge

correction and we applied Ripley's isotropic edge correction for all second-order summary statistics (Ripley, 1977).

The observed values of the second-order summary statistics were compared to corresponding values simulated by null models (Table 1). Simulations of null models create point patterns based on hypothetical assumptions of the underlying processes. If the null hypothesis is not rejected, the simulated data is statistically equivalent to the observed data. Deviations indicate that the processes of the observed point pattern are different to the assumed processes of the null model and these deviations must be interpreted in an ecologically meaningful way (Baddeley et al., 2015).

To investigate whether the pattern suggests a shift from a clustered to a regular pattern, we applied the null model of 'complete spatial randomness' (CSR) (Table 1). Under CSR we assumed that the trees are distributed randomly and independently within the plot without influencing the position of each other (Wiegand and Moloney, 2014). Deviations from the null model then indicate clustering of trees (increased number of neighbouring trees at one or several distances  $r$ ) or regularity of trees (less neighbouring trees at one or several distances  $r$ ). If the null model is not rejected, trees can be assumed to be distributed randomly at these distances (Velázquez et al., 2016). To detect a shift from a clustered pattern to a regular pattern with increasing tree height, we analysed the three height groups 'small', 'medium' and 'large' separately.

We tested association or segregation between small and large trees using the null model of 'antecedent condition' (Table 1), meaning that the null model kept the position of the large trees fixed while randomizing the distribution of the small trees. Antecedent conditions as a null model are appropriate if only one pattern influences the other, but not the other way around (Velázquez et al., 2016). This can be assumed for large trees influencing the spatial distribution of small trees. Possible outcomes are associations of small and large trees (increased number of small trees in the neighbourhood of large trees at one or several distances  $r$ ) or segregation of small and large trees (less small trees in the neighbourhood of large trees at one or several distances  $r$ ) or indifference with respect to the null model, i.e. the position of small trees is not influenced by the position of large trees (Velázquez et al., 2016). For the bivariate analyses, we considered only small and large trees because we assumed that association largely occurs as a result of nurse-protégé interactions between large trees and establishing seedlings or small saplings (Flores and Jurado, 2003).

Competition and facilitation were analysed using the null model 'random marking' (Table 1). In this null model, the tree heights were reassigned randomly to the trees without changing the tree positions. Thus, we did not investigate the spatial pattern of tree locations, but the result of post-establishment effects on the already existing pattern (Goreaud and Pellissier, 2003). Competition is indicated by a negative correlation of tree size at short tree-to-tree distances (mean tree height of two trees separated by distance  $r$  is smaller than the overall mean tree height), facilitation is indicated by a positive correlation at short tree-to-tree distances (mean tree height of two trees separated by distance  $r$  is larger than the overall mean tree height). No correlation (i.e. independent correlation) shows that the mean of two trees separated by distance  $r$  and the overall mean are identical (Wiegand and Moloney, 2014). For the nearest neighbour analysis competition is indicated by a positive correlation between the distance to the nearest neighbour and the size of the neighbour (Pielou, 1962). In contrast, a negative correlation indicates possible facilitation effects. For the nearest neighbour analysis of possible competition or facilitation effects, we analysed tree size both in terms of tree height and canopy area. For this, we used the absolute and not the classified height and canopy area values.

In order to assess deviations from the null models, ideally with high significance, we created simulated point patterns resulting from 1999 Monte Carlo simulations of the null models and calculated the desired summary statistics for each realization. The observed data represents the 2000th realization. We constructed pointwise simulation

envelopes based on these simulations by calculating second order summary statistics from the simulated point patterns and determining the 5th and 95th percentiles of these 1999 values of the summary statistics. A position of the observed summary statistic within the simulation envelope indicates no rejection of the null model (e.g. a random pattern for the null model of CSR). A position of the observed summary statistic (i.e. calculated from the observed data) above the simulation envelope indicates clustering or aggregation, whereas a position below the simulation envelope indicates regularity or segregation of the pattern. However, if the position is only slightly outside the simulation envelope, the results should not be overinterpreted (Wiegand and Moloney, 2014). Strictly speaking, this way of constructing the simulation envelopes means that for each distance  $r$  a separate test is performed. It is important to note that the simulation envelopes are no confidence intervals and bear the problem of multiple testing (Baddeley et al., 2014; Loosmore and Ford, 2006). Nevertheless, the envelopes are statistically valid and useful to assess what would have been the result of the test for several distances  $r$  (Baddeley et al., 2014). Due to the multiple testing problem and a possible resulting underestimation of the type I error, we additionally applied a goodness-of-fit test (GoF test) according to Loosmore and Ford (2006). The test summarizes the distance-dependent information of the summary functions to a single index by calculating the integrated squared deviation between the observed and the simulated data across all distances (Loosmore and Ford, 2006).

All data processing and analysis were performed in R 3.3.1 (R Core Team, 2017). For the spatial statistics we used the package *spatstat* 1.47-0 (Baddeley et al., 2015). All R-scripts can be found at [https://github.com/mhesselbarth/Hesselbarth\\_et\\_al\\_2018\\_JAE](https://github.com/mhesselbarth/Hesselbarth_et_al_2018_JAE).

### 3. Results

#### 3.1. Characterization of the plots

All plots varied in size, shape, number of trees/ha, mean tree size and species composition (Fig. 2 and Table 2, Appendix Fig. A5). This is because the plot area was not pre-set but depended on the tree density within the area (see section 2.2) and because we included only homogenous environmental conditions.

##### 3.1.1. Semi-arid savanna

In the open plot, the most abundant species was *Grewia flava* ( $n = 120$ ), followed by *Senegalia mellifera* subsp. *detinens* (synonym: *Acacia mellifera*;  $n = 47$ ). *Asparagus suaveolens* had a count of 32 individuals. *Lycium cinereum* ( $n = 28$ ), *Dichrostachys cinerea* ( $n = 23$ ) and *Vachellia erioloba* (synonym: *Acacia erioloba*;  $n = 13$ ) were less abundant. *Boscia albitrunca*, *Rhigozum trichotomum*, *Ehretia rigida*, *Aptosimum albomarginatum*, *Searsia burchellii*, *Vachellia luederitzii* (synonym: *Acacia luederitzii*) and *Ziziphus mucronata* shared the remaining 47 individuals (in decreasing order) (Appendix Fig. A6).

As in the open plot, in the dense plot the main species were *G. flava* ( $n = 165$ ) and *S. mellifera* ( $n = 162$ ). Species of intermediate

**Table 2**

Size of the plots and structural characteristics of the woody communities therein in the two different savanna types with open and denser woody vegetation.

	Semi-arid savanna		Mesic savanna	
	Open plot	Dense plot	Open plot	Dense plot
Plot area [ha]	0.70	0.51	0.14	0.03
Tree density [trees ha <sup>-1</sup> ]	499	962	3002	11541
Mean tree height [m]	1.4	1.7	0.5	1.1
Mean canopy area [m <sup>2</sup> ]	2.9	4.1	1.1	1.3
Number of tree species	13	10	13	32

abundance were *V. luederitzii* (n = 28), *L. cinereum* (n = 26), *S. burchellii* (n = 23) and *B. albitrunca* (n = 22). The remaining 65 individuals were shared between four more species (in decreasing order: *A. sua-veolens*, *R. trichotomum*, *E. rigida*, *V. erioloba*) (Appendix Fig. A6).

3.1.2. Mesic savanna

In the open plot, the most common species were *Vachellia nilotica* (synonym: *Acacia nilotica*; n = 136), followed by *D. cinerea* (n = 97) and *Vachellia karroo* (synonym: *Acacia karroo*; n = 86). Less common were *Diospyros lycioides* susp. *nitens* (n = 40) and *Searsia pallens* (n = 38). All remaining species had less than 10 individuals (in decreasing order): *Clerodendrum glabrum*, *Searsia pentheri*, *Olea capensis* subsp. *enervis*, *Dombeya rotundifolia*, *Searsia rehmanniana*, *Sclerocarya birrea* subsp. *caffra*, *Olea europaea* susp. *africana* and *Spirostachys afri-cana* (Appendix Fig. A7).

In the dense plot, the most common species was *O. europaea* susp. *africana* (n = 92), followed by *Euclea natalensis* with 44 individuals. *Vitex obovata* subsp. *obovata* (n = 31), *O. capensis* subsp. *enervis* (n = 29), *S. pallens* (n = 28), *S. africana* (n = 25), *Scolopia zeyheri* (n = 17), *D. cinerea* (n = 15), *Gymnosporia harveyana* (n = 13) and *Gymnosporia buxifolia* (n = 10) all had at least 10 individuals within the plot. Additionally, 22 species occurred with a very low abundance (n < 10) (Appendix Fig. A7).

3.2. Is the shift from a clustered to a regular pattern more pronounced in the semi-arid savanna and less pronounced in open vegetation?

3.2.1. Semi-arid savanna

In the open plot, there was clustering in all three height groups, especially at short distances  $r < 4$  m. The comparison of the height groups indicated that, at any given distance  $r$ , clustering tended to decrease with increasing tree height. Small trees were most strongly clustered (GoF test,  $p < 0.01$ ), while medium-sized trees showed a random or regular distribution for more distances  $r$  compared to small trees (GoF test,  $p < 0.01$ ). For large trees, the pattern was random for most distances  $r$  with the exception of clustering at short distances (GoF test,  $p < 0.001$ ). In the dense plot at short distances, clustering was present in all height groups. However, a decrease of clustering for distance  $r$  with increasing tree height was less distinct than in the open plot (Fig. 3). Small trees were clustered (GoF test,  $p < 0.001$ ), while for medium-sized trees the range of clustering increased to intermediate distances  $r$  (GoF test,  $p < 0.01$ ). For large trees, the range of clustering decreased again (GoF test,  $p < 0.001$ ), however, not as much as in the open plot (Fig. 3).

The mark-correlation function indicated that in the open plot the

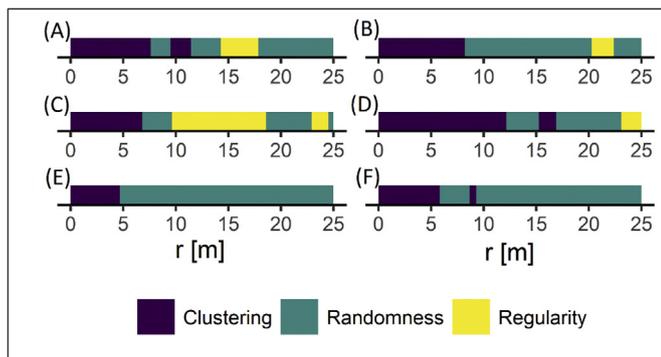


Fig. 3. Results of the pair correlation functions calculated for different height groups in the semi-arid savanna. The bars show distances  $r$  at which the spatial pattern of trees is clustered, random or regular. Results are shown for (A) small trees, (C) medium trees and (E) large trees in the open plot and (B) small trees, (D) medium trees and (F) large trees in the dense plot. The analyses were conducted using 1999 simulations of the null model of complete spatial randomness.

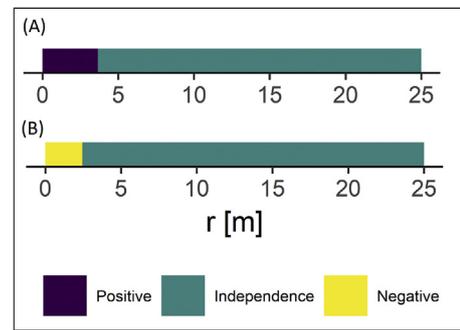


Fig. 4. Distances  $r$  at which the mark-correlation function indicated a positive, an independent or a negative correlation of the tree heights in (A) the open plot and (B) the dense plot of the semi-arid savanna. The bars indicate distances  $r$  at which positive, negative or no correlation between the marks is present. Calculations are based on the null model of random marking with 1999 Monte Carlos simulations. The null model keeps the position of the trees fixed while randomizing the height values.

mean tree height of neighbouring trees growing close together was greater than the overall mean. The mean height of neighbouring trees growing further apart was randomly distributed (GoF test,  $p < 0.01$ ). In the dense plot, close neighbours were of lower mean height than the overall mean height, but this was not statistically significant (GoF test,  $p > 0.05$ ) (Fig. 4).

Both canopy area and tree height increased significantly with increasing total distance to the four nearest neighbouring trees, but only in the dense plot. No statistically significant correlations were present in the open plot (Table 3).

3.2.2. Mesic savanna

In both the open and dense plot, there was clustering present, but clustering did not clearly decrease with increasing tree height. At short distance  $r$  clustering was present for small trees (open plot: GoF test,  $p < 0.01$ ; dense plot: GoF test,  $p < 0.001$ ). For medium-sized trees clustering was present for longer distances  $r$  (open and dense plot: GoF test,  $p < 0.01$ ). Also, for large trees, the distance  $r$  of clustering did not decrease and was present for larger distances compared to small trees (open and dense plot: GoF test,  $p < 0.001$ ) (Fig. 5).

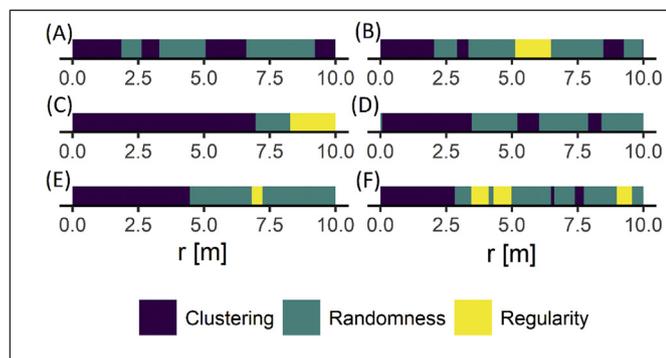
Trees growing close together had a greater mean tree height in the open plot (GoF test,  $p < 0.01$ ), whereas in the dense plot the mean tree height was smaller compared to the respective overall means (GoF test,  $p > 0.05$ ). The positive correlation at intermediate distances  $r$  in both plots should not be overinterpreted because the deviations from the simulation envelope were only marginal (see Appendix Fig. A3). However, the GoF-test was not statistically significant in the dense plot (Fig. 6).

In the open plot, both canopy area and height decreased with increasing distance to the four nearest neighbouring trees. In the dense plot, the height increased with increasing distance to the nearest neighbours (Table 4).

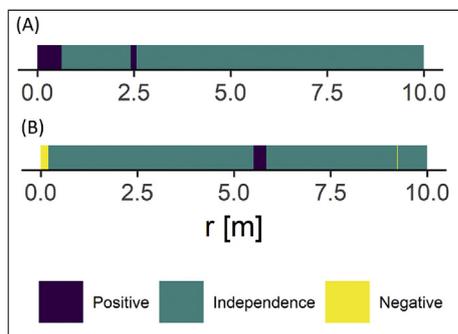
Table 3

Kendall's  $\tau$  correlation between the marks and the sum of the distances to the four nearest neighbours in the semi-arid savanna.

Plot type	Mark	Kendall's $\tau$	p-value
Open plot	Canopy area	0.07	0.066
	Tree height	-0.04	0.286
Dense plot	Canopy area	0.139	< 0.001
	Tree height	0.08	< 0.01



**Fig. 5.** Results of the pair correlation functions calculated for different tree height groups in the mesic savanna. Shown are the distances  $r$  at which a clustered, random or regular distribution of (A) small trees, (C) medium trees and (E) large trees in the open plot and (B) small trees, (D) medium trees and (F) large trees in the dense plot occur. The analyses were conducted for each height group separately using 1999 simulations of the null model of complete spatial randomness.



**Fig. 6.** Distances  $r$  at which the mark-correlation function indicated a positive, an independent or a negative correlation of the tree heights in (A) the open plot and (B) the dense plot of the mesic savanna. The bars show distances  $r$  at which positive, negative or no correlation between the marks is present. Calculations are based on the null model of random marking with 1999 Monte Carlos simulations. The null model keeps the position of the trees fixed while randomizing the height values.

**Table 4**

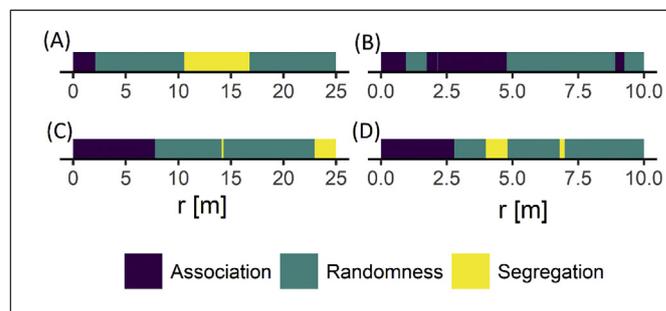
Kendall's  $\tau$  correlation between the marks and the sum of the distances to the four nearest neighbours in the mesic savanna.

Plot type	Mark	Kendall's $\tau$	p-value
Open plot	Canopy area	-0.12	< 0.001
	Tree height	-0.157	< 0.001
Dense plot	Canopy area	0.057	0.096
	Tree height	0.089	< 0.01

**3.3. Are associations between small and large trees present in the semi-arid and the mesic savanna and more pronounced in open vegetation compared to denser vegetation?**

**3.3.1. Semi-arid savanna**

The bivariate analysis revealed that in the open plot small trees were randomly distributed around large trees at almost all distances  $r$ . Only at very short distances  $r < 2$  m was association between small and large trees present. Segregation from large trees occurred at intermediate distances  $r$  (GoF test,  $p < 0.001$ ). In the dense plot, small trees were associated around large trees at longer distances  $r$  than in the open plot. Segregation was present for long distances  $r$ . At all other distances  $r$ , a random distribution was present (GoF test,  $p < 0.01$ ) (Fig. 7).



**Fig. 7.** Distances  $r$  at which the bivariate pair correlation functions indicated association or segregation between small and large trees for (A) the open plot and (C) the dense plot of the semi-arid savanna and for (B) the open plot and (D) the dense plot of the mesic savanna. The bars summarize the spatial pattern, showing the distances  $r$  at which association, segregation or randomness between small and large trees occur. Calculations are based on 1999 simulations of the null model of antecedent conditions, keeping the position of large trees fixed while randomizing the position of small trees.

**3.3.2. Mesic savanna**

In the open plot, small trees were associated with large trees at short and intermediate distances  $r$ . At all other distances  $r$ , the trees were randomly distributed (GoF test,  $p < 0.01$ ). Also, in the dense plot, association was present for short distances  $r$ , but at intermediate distances  $r$  we observed a segregation between small and large trees. At all other distances  $r$ , small and large trees were distributed randomly (GoF test,  $p < 0.01$ ) (Fig. 7).

**4. Discussion**

Hypothesis (i), which stated that the shift from a clustered to a regular pattern with increasing tree height is more pronounced in the semi-arid savanna was partly supported by the data. In the semi-arid savanna, small trees were clustered, whereas for medium and especially large trees the range of scales with clustering decreased and randomness increased. However, no height group showed a regular pattern at short distances. In contrast, the mesic savanna showed no shift from a clustered to a regular pattern with increasing tree height. Instead, the distances of clustering rather increased. Hypothesis (ii), which stated that the shift from a clustered pattern of small trees to a regular pattern of large trees is less pronounced in open vegetation was not supported. Even though evidence for competition was only present in the dense plots, no clear differences were observed between open and denser vegetation. Hypothesis (iii), which stated that associations between small and large trees can be found in both savanna types was supported by the data. Associations were present in open and dense vegetation across sites for short distances. Hypothesis (iv), which stated that associations of small and large trees are more prevalent in open vegetation due to less important competition effects was not supported by the data. Associations were present in all sites and across plots and even more pronounced in dense vegetation.

**4.1. Spatial patterns in the semi-arid savanna**

In the semi-arid savanna, both the open and dense plots exhibited short-scale clustering of trees, especially among small individuals. In the medium and large height groups, the corresponding patterns approached a more random distribution. However, no pattern was regular. This is in line with other studies reporting a tendency towards clustering, especially of small savanna trees (Caylor et al., 2003; Meyer et al., 2008; Mureva and Ward, 2016). One possible explanation is a limited and concentrated seed dispersal and the sharing of suitable regeneration sites for establishment and growth (Caylor et al., 2003; Meyer et al., 2008). For example, Joubert et al. (2013) report that seeds

of *S. mellifera*, one of the predominating species at the semi-arid study sites, are mostly found in the sub-canopy area (Joubert et al., 2013). Similarly, the fleshy fruits of the other abundant species, *G. flava*, are mainly distributed by birds, which perch in the canopy of larger trees and drop the undigested seeds into the sub-canopy area (Tews et al., 2004). In the open plot, clustering and association could have been further promoted by facilitation effects (Meyer et al., 2008). Evidence for possible facilitation effects, such as a higher soil moisture and nutrient concentrations (Flores and Jurado, 2003), were the above-average size of trees growing close together in combination with sufficient height differences to allow large trees to facilitate small trees (Schleicher et al., 2011).

It has been frequently observed that with increasing tree size competition between trees increases (Sea and Hanan, 2012) and that the chance of survival decreases with decreasing distance to other trees (Joubert et al., 2013; Tews et al., 2004). This may lead to density-dependent mortality of small trees as they grow and consequently to less clustering of large trees. The random spatial distribution of the surviving large trees may then be formed by the random distribution of regeneration sites where trees had been able to grow and survive (Caylor et al., 2003). In the open plot, no evidence for competition was present. The distances between the large trees can be assumed to be large enough to exclude further density-dependent mortality. Hence, over time, a further shift in the pattern towards regularity would be unlikely. Consequently, competition seemed not to be strong enough to lead to segregation of small and large trees. Contrastingly, in the dense plot, the lack of a regular pattern does not necessarily mean that no density-dependent mortality is taking place beyond the seedling stage (Couteron and Kokou, 1997). Here, evidence for competition was present with trees growing close together being of smaller size. It is possible that the pattern had already shifted from clustered to random in the past, while a regular pattern may still develop in the future if tree-tree competition is still strong enough (Couteron and Kokou, 1997). Interestingly, associations between small and large trees were present up to larger tree-to-tree distances in the dense plot compared to the open plot. This suggests limited seed dispersal as a major process for the spatial patterning of trees that overrides possible competition effects.

Another factor that could have contributed to the observed spatial patterning is disturbance. The high abundance of *G. flava* indicates that the vegetation within the open plot was exposed to some sort of bush control in the past, selectively thinning-out undesirable species such as *S. mellifera* for the benefit of trees attractive to browsing herbivores (Harmse et al., 2016). This could have reduced tree-tree competition and consequently a density-dependent shift from a clustered to a regular pattern. Likewise, natural disturbances, such as prolonged droughts, could have been a contributing factor preventing such a shift, as well as segregation between small and large trees (Sea and Hanan, 2012). Disturbances may have induced the death of whole cohorts of trees, reducing overall tree-tree competition.

To summarize, at both plots tree-tree interactions and especially limited seed dispersal were likely factors that could explain the observed spatial patterns of trees at short tree-to-tree distances. However, different tree densities may select factors differently or alter the combinations of factors. In other words, while evidence for competition was only present at the dense plot, facilitation was only likely at the open plot. At larger tree-to-tree distances, the distribution of regeneration sites may be a primary factor driving the patterns.

#### 4.2. Spatial patterns in the mesic savanna

In the mesic savanna, clustered patterns for short tree-to-tree distances were present at both plots and across height groups. With increasing tree size, the pattern neither expressed a random nor a regular characteristic. Rather, the distances of clustering increased. As in the semi-arid savanna, a reason for the clustering could be limited seed dispersal, and consequently accumulation of dispersules close to the

parent tree. Walters and Milton (2003) showed that the amount of seeds decreases with increasing distance to the stem of *V. karro* and *V. nilotica* (Walters and Milton, 2003), the two predominant species at the mesic site. Facilitation effects explaining the clustering were not distinguishable from other possible processes leading to clustering, even though spatial proximity corresponded with a superior growth in the open plot. The size difference between the height groups did not differ a lot, and hence not all large trees were necessarily able to provide classical facilitative effects on what was considered small trees (Schleicher et al., 2011).

In mesic savannas, competition for water is assumed to be less important than in semi-arid savannas because of the generally higher MAP (Sankaran et al., 2005; Vadigi and Ward, 2013). Nevertheless, competition for light and a reduced growth due to shading may still be present (Midgley and Bond, 2001; Vadigi and Ward, 2013). With increasing tree size the competition for light increases (Sea and Hanan, 2012) and a trend towards a regular pattern should become evident (Wiegand et al., 2006). A possible explanation as to why such a shift was not observed may be disturbances reducing tree-tree competition, and hence reducing density-dependent mortality (Sea and Hanan, 2012). Fire is a more frequent disturbance in mesic savannas than in semi-arid savannas (Sankaran et al., 2005) and is known to lead to clustering of woody trees (Accatino et al., 2016; Skarpe, 1991). Tree clusters with a high local canopy cover suppress the grass production, and thus the fuel load for fires in the sub-canopy (Scholes and Archer, 1997). The superior size of trees with short tree-to-tree distances in the open plot could be evidence for this protection against fire. In the dense plot, there was some evidence for competition at short tree-to-tree distances, but clustering increased with increasing tree size and association between small and large trees occurred. This suggests that although tree-tree competition was present, trees may have benefitted from clustering as it reduces the likelihood of being affected by localized fire events (Accatino et al., 2016; Skarpe, 1991), which may override negative competition effects. In addition, limited seed dispersal (Walters and Milton, 2003) was a likely reason for the association (compare section 4.1). Therefore, a regular pattern is unlikely to develop at the mesic savanna. Thus, a competition-driven segregation of small and large trees seems to be rather unlikely and clustering due to limited seed dispersal and disturbances may have been the primary drivers of spatial patterning. Also, Pillay and Ward (2012) found mainly clustered patterns of trees in another mesic savanna, even though evidence for competition was present (Pillay and Ward, 2012). They concluded that limited seed dispersal, environmental heterogeneity or disturbances may be more important than density-dependent mortality (Pillay and Ward, 2012).

To summarize, in the mesic savanna it was likely that especially seed dispersal influenced the spatial patterning of trees at short tree-to-tree distances in both open and dense vegetation. In the dense plot, competition was another possible driver, albeit probably less important. Finally, density-dependent differences between the two plots seemed to be less pronounced. Disturbances such as fire seemed to be more important at larger tree-to-tree distances and may be another crucial driving factor of the patterning.

#### 4.3. Limitations of the approach

Point pattern analysis can be a powerful tool to gain information about ecological processes from the observed distribution patterns of individuals, albeit it can be difficult to link patterns and processes (Wiegand and Moloney, 2014). One possibility to improve the pattern-process link would be to include a temporal scale (Meyer et al., 2008) to determine if the pattern of large trees represents a steady state or if a shift from clustered to regular is still ongoing. Furthermore, a combined experimental approach would be desirable to verify the conclusions about competition and facilitation made in this study. Nevertheless, point pattern analysis is a good alternative to experimental approaches

for examining tree-tree interactions, especially if the assumed interactions and processes are slow (Meyer et al., 2008). We assumed that the tree density was a confounding factor influencing possible tree-tree interactions. Yet, the lower tree densities in the open plots may also be a results of past competition and not just due to the factors influencing the interactions. Further, even though we assumed homogeneous study sites, additional data about the fine-scale environmental conditions (e.g. in soil properties, fuel loads) or species-specific growth requirements and seed dispersal distances could help to draw conclusions based on the point pattern in the savanna types. Additionally, environmental conditions other than climate may also be influential and different across savanna types. This would interfere with our interpretations of the data. Therefore, further environmental data could be used to either incorporate or exclude possible confounding factors. In the mesic savanna, the differences between the height groups were marginal, making interpretations difficult. Also, especially the common *Vachellia* species resprout intensively after fire damage or herbivory (Hean and Ward, 2012). This may introduce a measuring bias because the distinction between multi- and single stemmed individuals may be wrong (Ebert and McMaster, 1981). Vegetative propagation may introduce a similar bias. Lastly, even though we tried to sample savanna vegetation with a minimum of human disturbances, this does not imply that the study sites were necessarily representative of natural semi-arid or mesic savannas in general. However, we are nevertheless confident that the addressed processes of tree-tree interactions take place in similar ways in savanna systems elsewhere with comparable environmental settings. In order to account for different plant communities, we suggest that further studies take a closer look at species-specific functional traits of the most abundant tree species and bivariate or even multivariate point pattern analysis considering different tree species.

## 5. Conclusions

The aim of the study was to gain a better understanding of the spatial patterning of trees in relation to tree density, comparing a semi-arid and mesic savanna in two nature reserves in South Africa. The still incomplete understanding of savanna dynamics highlights the need for a better insight into processes and tree-tree interactions shaping the vegetation structure.

We showed that tree-tree interactions are present in savannas, at different spatial scales and in relation to tree density. Naturally, the resulting patterns have an influence on the co-dominance of trees and grasses due to changes in tree-grass competition and facilitation. In other words, the specific competitive environment emanating from the overall tree-grass and tree-tree interactions can be understood as a compound factor influencing the vegetation structure (including composition) in space and time. Therefore, to improve the understanding of savanna dynamics, tree-tree interactions across demographic stages also need to be considered. The results of the point-pattern analysis suggest that both savanna type (semi-arid and mesic) and tree density (open and dense) have an influence on savanna dynamics. Competition effects were mainly found in dense vegetation. Contrastingly, facilitation seemed to be more common in open vegetation. Besides competition and facilitation other factors, such as seed dispersal or fine-scale environmental heterogeneity, can also have considerable influence on the patterns. Seed dispersal may play a role at short tree-to-tree distances, whereas at larger tree-to-tree distances, environmental heterogeneity may be superior in the semi-arid savanna and disturbances in the mesic savanna. The different tree densities seem to have a larger influence on the patterns and processes in the semi-arid savanna compared to the mesic savanna. This is an important result and it can be concluded that savanna studies should take actual tree densities into account, especially if different savanna types are compared. Therefore, we suggest considering tree densities as a possible confounding factor for further study designs.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2018.06.002>.

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